



A THIRD INCUBATION TACTIC: DELAYED INCUBATION BY AMERICAN ROBINS (*TURDUS MIGRATORIUS*)

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ABSTRACT.—Birds generally begin incubation either before laying the last egg of a clutch or when the last egg is laid. We report a third incubation tactic, in which incubation onset is delayed beyond the laying of the last egg. In an Illinois population of American Robins (*Turdus migratorius*), ~20% of females delayed the onset of incubation ≤ 4 days beyond clutch completion. Females that delayed incubation nested earlier and took longer to hatch their young than those that initiated incubation before or on the clutch completion date. Using a cost–benefit approach, we propose that predictably low levels of predation at the study site may have reduced the costs associated with delaying incubation. Females do not appear to pay any fitness costs associated with delaying incubation and may benefit by replenishing food reserves early in the season, when the energetic demands of incubation are higher. Alternatively, females may benefit by delaying incubation as a means of timing the hatching of young with availability of food resources. Although this delayed incubation may be attributable to the unique conditions of the study site, we suggest that this behavior may be found more widely, particularly in populations experiencing similar reductions in predation risk, such as populations in urban areas. Received 27 December 2007, accepted 12 September 2008.

Key words: American Robin, delayed incubation, predation risk, resource availability, *Turdus migratorius*.

Una Tercera Táctica de Incubación: Incubación Retrasada en *Turdus migratorius*

RESUMEN.—Las aves generalmente inician la incubación ya sea antes de poner el último huevo de una nidada o cuando ponen el último huevo. Documentamos una tercera táctica de incubación, en la que el inicio de ésta se retrasa después de la postura del último huevo. En una población de *Turdus migratorius* de Illinois, cerca del 20% de las hembras retrasaron el inicio de la incubación por cuatro o más días después de completar la postura. Las hembras que retrasaron el inicio de la incubación anidaron más temprano y sus pichones tardaron más tiempo en eclosionar en comparación con las hembras que iniciaron la incubación en el día en que terminaron su postura o antes. Usando un enfoque de costo-beneficio, proponemos que los niveles de depredación predicablemente bajos que existen en el sitio de estudio podrían haber reducido los costos asociados con el retraso de la incubación. Las hembras no parecen pagar ningún costo en términos de su adecuación asociado con el retraso de la incubación y podrían beneficiarse abasteciéndose de reservas de alimento al inicio de la temporada, cuando las demandas energéticas de la incubación son mayores. Alternativamente, las hembras podrían beneficiarse retrasando la incubación como una manera de sincronizar la eclosión de los pichones con la abundancia de recursos alimenticios. Aunque la incubación retrasada podría ser atribuible a las condiciones únicas del sitio de estudio, sugerimos que este comportamiento podría encontrarse más frecuentemente, particularmente en poblaciones que experimentan reducciones similares en el riesgo de depredación, como las poblaciones de áreas urbanas.

BY VARYING THE timing of the start of incubation, birds exert substantial control over when their eggs hatch, which can affect the fitness of those eggs (Clark and Wilson 1981, Slagsvold 1986, Ricklefs 1993). Delaying incubation until all the eggs are laid increases hatching synchrony but exposes the earlier-laid eggs to predation risk for a longer time. Conversely, initiating incubation before clutch completion increases hatching asynchrony but reduces predation risk for eggs laid early. Birds are thought to use

one of two incubation tactics: initiating incubation (1) when the last egg is laid or (2) before the last egg is laid (Stoleson and Beissinger 1995, Hébert 2002). Here, we report a third tactic exhibited by American Robins (*Turdus migratorius*), whereby females delay the onset of incubation beyond the day the last egg is laid.

Initiation of incubation before clutch completion is the more common pattern in birds, particularly in species with altricial young (Clark and Wilson 1981, Hébert 2002) and those in temperate

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environments (Slagsvold 1986). Beginning incubation when the clutch is complete is less common, occurring most often in species with precocial young (Ricklefs 1993). There are many exceptions to these general patterns, however, and many orders have species in both categories (e.g., Anseriformes, Charadriiformes, Piciformes, and Passeriformes; Ricklefs 1993, Hébert 2002). However, we are unaware of any studies of either altricial or precocial birds that have reported a delay in incubation onset of >24 h beyond clutch completion. In addition to documenting the occurrence of this incubation behavior in American Robins, we evaluate whether ambient temperature or clutch completion date affect the timing of incubation onset. We also examine the fitness consequences of each incubation tactic as it relates to hatching and fledging success. Finally, we discuss how predation risk and food availability may play a role in shaping the timing of incubation in this population of American Robins.

METHODS

We studied an individually marked population of American Robins nesting in a mixed-species coniferous Christmas-tree farm near Champaign, Illinois, in 2003 and 2004 (40°02'N, 88°10'W; Rowe and Weatherhead 2007). The maximum height of the trees is ~2.5 m. Female American Robins build an open-cup nest and lay a clutch of three to four eggs. Their incubation period has been reported to be 11–14 days (Howell 1942 and references therein). Females incubate alone, but both parents provision nestlings and defend the nest from predators (Weatherhead and McRae 1990, Sallabanks and James 1999). Incubation onset is reported to begin sometime after the second egg is laid (Sallabanks and James 1999) but generally before all the eggs have been laid.

We searched systematically for nests on the entire site every three days. Once located, nests were monitored daily (between 0500 and 1500 hours CST) through the fledging of offspring ($n = 128$ nests, 50 in 2003 and 78 in 2004). We established “clutch initiation date” as the date we observed the first egg in the nest. Here, we consider only nests we found before the second egg was laid. To evaluate the fitness consequences of each incubation behavior, we recorded the proportion of eggs that hatched and the proportion of young that fledged from each nest.

During nest checks prior to hatching, we noted the number of eggs and checked whether the female was incubating by touching the eggs to see if they were warm. We defined “onset of incubation” as the date we first detected warm eggs in the nest. We classified nests on the basis of our estimate of incubation onset in relation to clutch completion date: before, on, or after. We were confident in our assignment of the onset of incubation because once eggs were first recorded as being warm they were always warm on subsequent visits. To confirm the accuracy of our estimates of incubation onset independently, however, we compared the date of clutch completion with the date the first egg hatched. If our estimate of incubation onset was accurate, the time between clutch completion and hatching should increase progressively from clutches incubated before clutch completion, to clutches incubated at clutch completion, to clutches where incubation was delayed beyond clutch completion.

To evaluate whether ambient temperature was associated with incubation patterns, for each nest we recorded the mean temperature (°C) on the day of clutch completion using local weather

data for Champaign (Illinois State Water Survey, Champaign), recorded 4 km northwest of the study site. We also evaluated whether weather conditions during the years of our study differed significantly from normal conditions in the area by comparing daily mean temperature from 2003 and 2004 with the normal daily mean temperature of the area. Normal daily mean temperatures were based on a 30-year average (1971–2000).

Multiple-brooding was common in this population (Rowe and Weatherhead 2007), so, to avoid pseudoreplication, we included data from only one clutch of a given pair within each season, preferentially selecting clutches with complete nesting data. In cases where the same female bred in both years ($n = 14$), we randomly excluded data from one of the years.

All statistical analyses were performed using SPSS, version 11.0 (SPSS 2005). We used analyses of variance (ANOVA) to evaluate the accuracy of our estimates of the onset of incubation and to evaluate the fitness consequences of each incubation-onset category. *Post-hoc* tests for differences between incubation-onset categories were performed using Scheffe's test. We used Pearson correlation to test whether temperature patterns during our study were significantly different from normal. We used multinomial logistic regression to evaluate the relationships between temperature, clutch completion date (independent, continuous variables), and the category of incubation onset (dependent, categorical variable). Because an exploratory analysis revealed differences between years in the relationship between temperature and incubation onset, we analyzed each year separately. Values are reported as means \pm SE, all tests are two-tailed, and we assumed significance when $P < 0.05$.

RESULTS

The timing of incubation onset ranged from two days before to four days after clutch completion (Fig. 1), with 57.8% of females (74 of 128) initiating incubation before clutch completion, 22.7% (29 of 128) on the day the clutch was complete, and 19.5% (25 of 128) after clutch completion.

Our estimates of incubation onset reliably predicted the time between clutch completion and hatching, thus validating the reliability of those estimates; the time from clutch completion to hatching increased across our incubation categories (ANOVA: $F = 11.64$, $df = 2$ and 98, $P < 0.001$; Fig. 2). Following clutch completion, the eggs of females that initiated incubation after clutch completion took significantly longer to hatch (12.6 ± 0.3 days) than those that initiated incubation on (11.5 ± 0.1 days; Scheffe test: $P = 0.008$) or before clutch completion (11.2 ± 0.1 days; $P < 0.001$). Although there was less time between clutch completion and hatching for females that began incubating before clutch completion than for females that began on the date of clutch completion, the difference was not significant ($P = 0.31$). Among individual nests, the longest incubation delay we recorded was 4 days after clutch completion, and that nest took 13 days from clutch completion to hatching. The time from clutch completion to hatching was similar in both years of the study (2003, 11.4 ± 0.1 days; 2004, 11.5 ± 0.2 days; t -test: $t = 0.57$, $df = 99$, $P = 0.57$).

Females using different incubation behaviors did not differ significantly in the number of young hatched (ANOVA: $F = 0.75$, $df = 2$ and 125, $P = 0.47$) or in the number of young fledged ($F = 1.64$, $df = 2$ and 107, $P = 0.20$), which suggests that females that delayed the

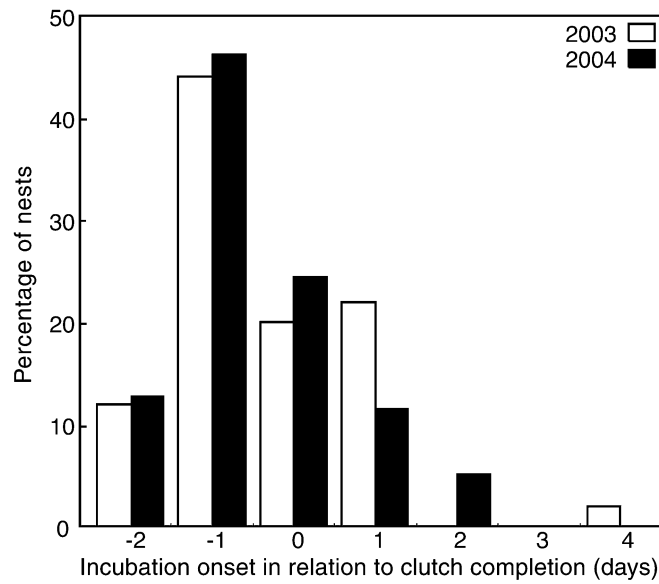


FIG. 1. Distribution of American Robin nests based on the timing of incubation onset in relation to clutch completion date in 2003 ($n = 50$) and 2004 ($n = 78$).

onset of incubation did not suffer a fitness cost compared with those that initiated incubation before or on the clutch completion date.

Daily mean temperatures during the years of our study were significantly correlated with normal daily mean temperatures, which suggests that the years of our study did not differ from normal

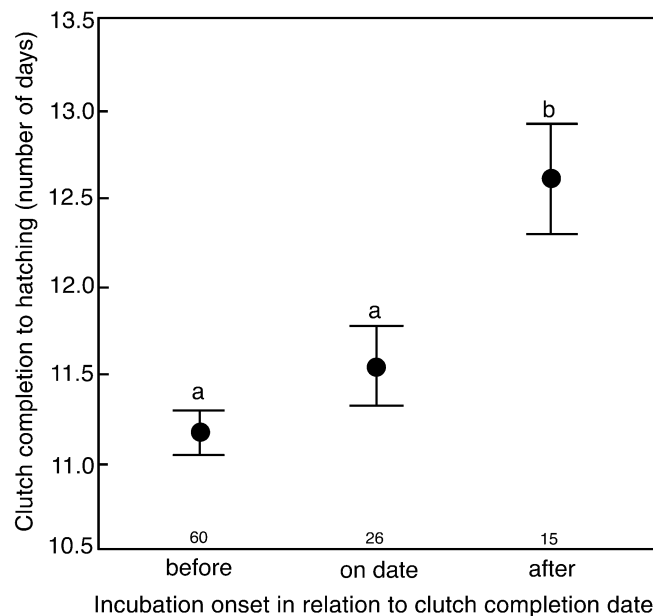


FIG. 2. Average number of days (\pm SE) from clutch completion to hatching in American Robins based on the timing of incubation onset (before, on, or after clutch completion date) in 2003 and 2004. Significant differences between categories (based on a *post-hoc* Scheffe test) are represented by different letters above the error bars. Sample sizes are given below error bars.

temperature patterns in the area (Pearson correlation: 2003, $r = 0.70$, $P < 0.001$; 2004, $r = 0.68$, $P < 0.001$, $n = 122$ for both). The relationship between temperature and incubation category differed between years of the study (ANOVA: $F = 4.10$, $df = 2$ and 122 , $P = 0.02$). Therefore, we performed a separate analysis for each year. There was no relationship between temperature and incubation onset category in 2003 (multinomial logistic regression: $\chi^2 = 1.70$, $P = 0.43$, $n = 50$). There was a significant relationship in 2004 ($\chi^2 = 11.84$, $P = 0.003$, $n = 78$) whereby the temperature on the day of clutch completion was cooler for females that initiated incubation after clutch completion ($13.7 \pm 1.7^\circ\text{C}$) than for those initiating before ($19.0 \pm 0.8^\circ\text{C}$) or on the day of clutch completion ($20.6 \pm 1.7^\circ\text{C}$).

Daily mean temperature increased through the 2004 breeding season (linear regression: $R^2 = 0.38$, $F = 72.20$, $df = 1$ and 120 , $P < 0.001$), which suggests a relationship between the timing of breeding within the season and the timing of incubation onset. When clutch completion date is incorporated into the model of the relationship between temperature and category of incubation onset for females nesting in 2004, clutch completion date becomes a strong predictor of incubation-onset category ($\chi^2 = 8.70$, $P = 0.01$) and temperature is no longer significant ($\chi^2 = 0.006$, $P = 1.00$; diagnostic tests did not reveal a significant violation of the assumption of no collinearity between the predictor variables temperature and clutch completion date: tolerance = 1.0, variance inflation factor [VIF] = 1.0). In 2004, females delaying the onset of incubation until after clutch completion tended to nest earlier in the breeding season (calendar date = 126 ± 5 days) than those beginning incubation before (140 ± 3 days) or on (151 ± 3 days) the clutch completion date (Fig. 3). We did not find the same relationship between clutch completion date and incubation-onset category for females nesting in 2003 ($\chi^2 = 5.72$, $P = 0.06$). There was, however, great variation in incubation-onset tactics in 2003

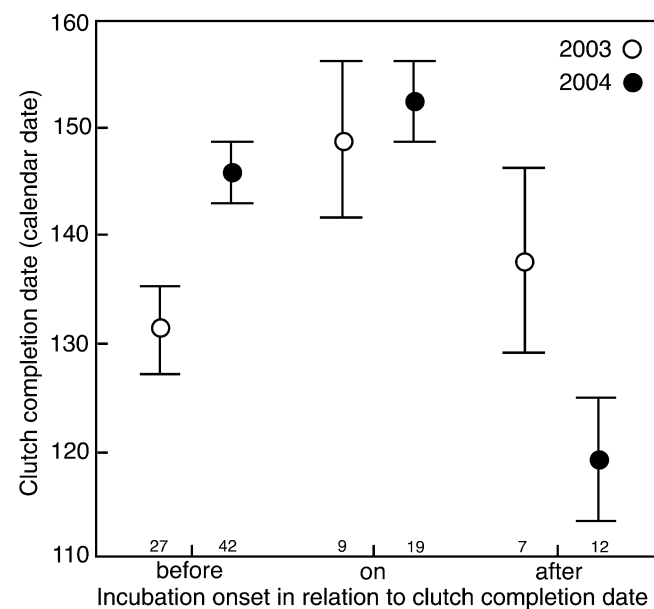


FIG. 3. Average calendar date (\pm SE) when clutches were completed in American Robins based on the timing of incubation onset (before, on, or after clutch completion date) in 2003 and 2004. Sample sizes are given below error bars.

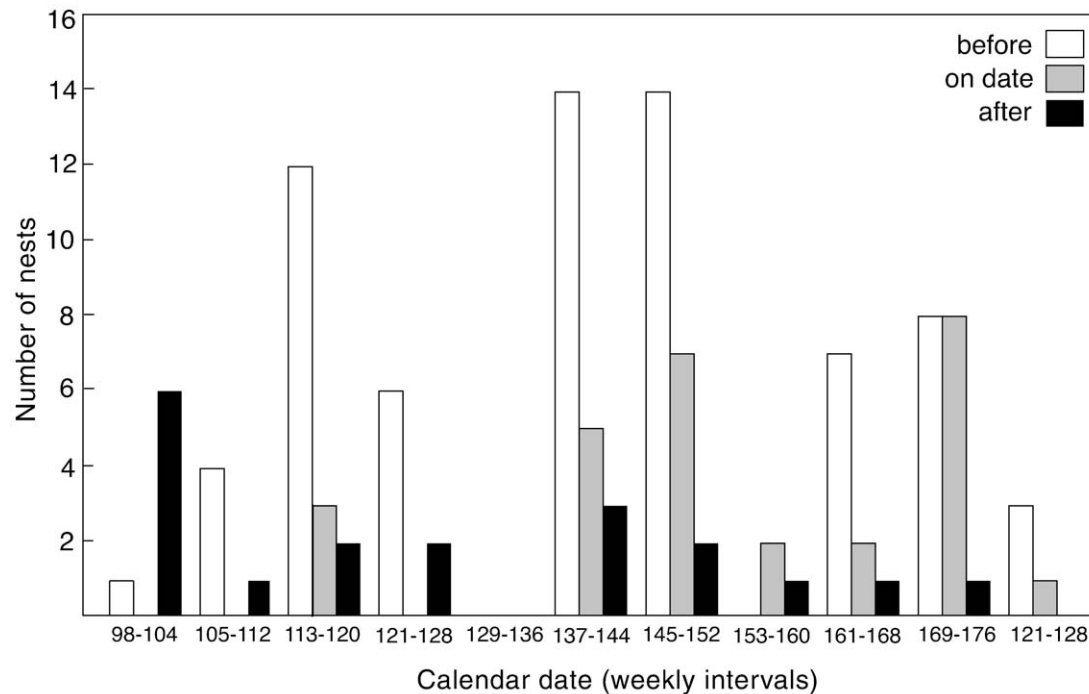


FIG. 4. Distribution of the timing of incubation onset (before, on, or after clutch completion date) of nesting American Robins in 2003 and 2004 in relation to calendar date (grouped into weekly intervals). Calendar date 98 corresponds to 8 April.

and 2004, with females exhibiting all three tactics throughout the breeding season (Fig. 4).

Given that females nesting early in the season also tended to delay the onset of incubation, the longer time from clutch completion to hatching may have been the result of nesting earlier in the season rather than of delayed incubation *per se*. For example, higher energetic costs of incubation early in the season could have caused females to take more incubation breaks, thereby prolonging the incubation period. Were this the case, we would expect the time from clutch completion to hatching to decline over the season for females that initiated incubation before or on the clutch completion date. Although we found a trend in the predicted direction, the small amount of variation explained by season was statistically nonsignificant (linear regression: $R^2 = 0.04$, $df = 1$ and 84 , $P = 0.06$). Therefore, there appears to be little direct effect of season on the duration of incubation.

DISCUSSION

We have described a previously unreported behavior of American Robins delaying incubation onset beyond clutch completion, exhibited by ~20% of the population and found most commonly in early breeders. Although this phenomenon may be attributable to the unique conditions at the study site, it is also possible that it occurs in other species and locations but has not been detected.

Understanding why some American Robins do not begin incubation until some time after clutch completion actually involves two questions: what advantages might they realize and why does it occur in our study population? The fact that American Robins were more likely to delay incubation early in the season suggests two possible advantages. The first is that females that delay

incubation can forage for a day or more and replenish energy reserves needed during incubation. Cooler temperatures would make incubation more energetically expensive early in the season (White and Kinney 1974, Williams 1996, Tinbergen and Williams 2002), potentially explaining why more females delayed incubation early in the breeding season. However, if clutch completion date were the only factor associated with patterns of incubation onset, we would predict that females nesting at the same time should employ the same behavioral tactic. This was not the case. We found that females exhibited all three incubation tactics throughout the season, which suggests that individual condition may also play a role in shaping behavioral patterns of incubation.

The second possible advantage is related to the fact that delaying incubation also delays hatching. Resource availability often varies through the breeding season (Martin 1987, Nagy and Holmes 2005), creating selection on birds to time hatching with predictable availability of resources (Lack 1954, Meijer et al. 1999, Visser et al. 2006, Barea and Watson 2007). Early in the season, birds take longer to build nests and to start laying eggs once nests are built and are more likely to abandon nests without laying eggs (Stutchbury and Robertson 1987, Teather et al. 1988, Maddox and Weatherhead 2006). Although we found no fitness costs associated with delaying onset of incubation, determining whether delayed incubation and these other behaviors are adaptations female birds use to help match the timing of hatching with resource availability will require designing experiments that allow delaying or accelerating the timing of hatching, particularly for early-season nests.

One reason that delayed incubation occurred in our study population may be that the risk of nest predation was relatively low. When risks are high, females should minimize the time that

young (both eggs and nestlings) are in the nest and most vulnerable to predation (Clark and Wilson 1981, Ricklefs 1993, Stoleson and Beissinger 1995); this would favor starting incubation before clutch completion. In our population, overall predation was 29.7% (38 of 128 nests), with only 7 nests (5.5%) depredated before or during incubation. Furthermore, ~60% of the total predation occurred on four nights in 2004, likely because of a transient Coyote (*Canis latrans*; see Maddox and Weatherhead 2006). If such episodic events are rare, predation risk may be very low. This is probably a result of the study site being surrounded by corn and soybean fields that do not support nest predators. Predictably low predation risk reduces the costs associated with delaying the onset of incubation after clutch completion. If the benefits of delayed incubation, such as optimally timing hatch with availability of food resources, are greater than the costs, including increased risk of predation, then delaying incubation would be favored.

The cost–benefit hypothesis for delayed incubation assumes that females can evaluate predation risk before any predation occurs. This is most likely to occur in females that breed on the same site in multiple years. American Robins often return to the same breeding site between years (Weatherhead and McRae 1990, Haas 1997, Rowe and Weatherhead 2007), which suggests that older females would have the opportunity to evaluate predation risk in one year and modify their nesting behavior the following season. We therefore expect females that delayed incubation onset until after clutch completion to be older and to have bred on the site previously. Our sample sizes were too small, however, and we had insufficient age data for the birds to evaluate this hypothesis.

Although levels of predation in our study population were generally low, other populations also experienced reduced predation risk (e.g., in urban populations; Gering and Blair 1999, Anderies et al. 2007). If these populations also benefit from delaying the onset of incubation, this tactic may be more widespread. The range of “incubation” period (completion of egg laying to first egg hatching) in our population of American Robins, including females that delayed the onset of incubation, was 9–15 days. This is somewhat broader than the range of incubation periods reported elsewhere for American Robins (11–14 days; Schantz 1939, Howell 1942 and references therein). Given that our range is based on a much larger sample than those earlier studies (e.g., Howell 1942, $n = 17$ eggs), however, it is possible that delayed incubation occurs infrequently in other populations. Ornithological studies often report considerable variation in incubation duration, so delayed incubation could occur in other species but go undetected. We found an anecdotal report of delayed incubation in Eastern Bluebirds (*Sialia sialis*), where incubation did not begin until ~12 h after clutch completion (Hamilton 1943). Identifying delayed incubation will often be difficult, because, in many field studies, nests are often found after onset of incubation. Studies in which nests are found before incubation and in which daily nest checks are combined with temperature–data loggers in the nest would be particularly informative regarding the generality of this behavior.

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